

## ECHOES OF ULTRASONIC PULSES FROM FLYING MOTHS

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It has been firmly established by Griffin, Webster and Michel (1960) that flying bats use echolocation in tracking and capturing flying insects. By this means *Myotis lucifugus* is able to detect insects as small as *Drosophila melanogaster* at distances as great as 50 cm. These authors also used acoustic jamming experiments to show that under these circumstances the bat's clue to the presence of an insect is the echo of its ultrasonic cry rather than the sonic output from the vibrating wings of the prey. However, they reaffirmed the observation made by others (Möhres, 1950; Kolb, 1959; Treat, 1955) that bats at rest and not emitting ultrasonic orientation sounds will respond quickly and accurately to the nearby presence of a buzzing insect.

The ability of *Myotis* to determine the distance, direction, and presumably the size of an object as small as *Drosophila* at a distance of 50 cm. suggests that bats might be able to discriminate many other characteristics of larger prey, such as moths, through the properties of their echoes. Most observers of bat behavior have at one time or another tossed pebbles or other inert objects to feeding bats. In the field bats will commonly detect and track such objects, but rarely attempt to attack or capture them. Under laboratory conditions bats can be trained to track and capture non-flying objects such as mealworm larvae tossed in the air (Webster, 1963), but under natural conditions it seems unlikely that they ever encounter potential prey that is not flapping its wings. Although the wing sound seems to be unimportant as a clue (Griffin, Webster and Michel, 1960), it seems possible that the wing movement of the prey may modify the echoes returning to a flying bat and enable it to discriminate a flying insect from a pebble. This possibility was first pointed out by Griffin (1958).

Further indirect evidence in favor of this hypothesis is the often-made observation (*e.g.*, Treat, 1955; Roeder, 1962) that "freezing" is one of the many types of response made by moths to the proximity of bats or when exposed to ultrasound. Under field conditions some moths (and lacewings) cease all flight movement and drop to the ground when exposed to a source of ultrasonic pulses. In one sense this maneuver might be expected to simplify the bat's task of tracking its prey, since the tracker is presented with a target falling in a roughly ballistic and therefore more predictable trajectory compared with a moth's flight path. Since "freezing" behavior can be presumed to have some survival value to the moth, this disadvantageous aspect (to the moth) is possibly offset by the attainment of some degree of acoustic concealment. In passing, it should be pointed out that exposure to a series of bat-like sounds just as frequently causes moths to make a variety of violent evasive maneuvers or to fly directly away from the source (Roeder, 1962). It is the age-old question of whether it is best to duck.

dodge, or run, to which the answer seems to be that there is survival value in variety.

At present there seems to be no direct way of finding out how much information a bat obtains from echo fluctuations produced by the wing movements of its prey. In the following experiment the bat was replaced by a source of ultrasonic pulses and a microphone in order to determine how the amplitude and other properties of the echo are affected by the wing movements of flying moths.

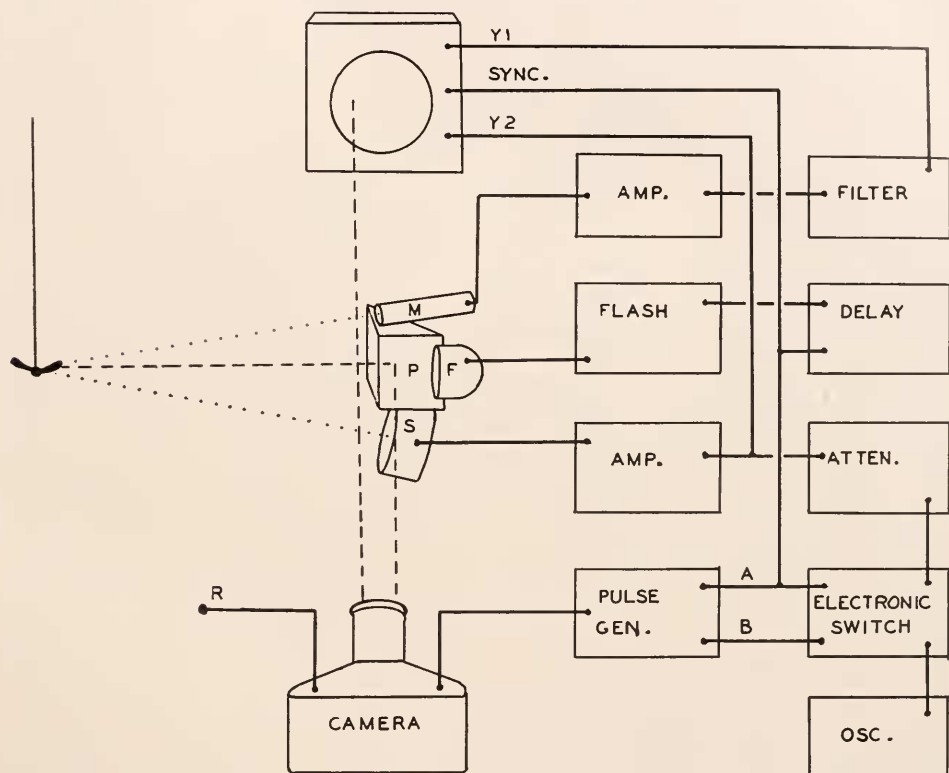


FIGURE 1. Block diagram of apparatus used to record the attitude and echo of a moth in fixed flight. Dotted line, acoustic path; dashed line, optical path. or other details see text.

#### METHOD

A block diagram of the apparatus is shown in Figure 1. In the early experiments a 35-mm. camera (Exakta) equipped with a 180-mm. telephoto lens framed the tube face of an oscilloscope at a distance of one meter. Half the image of the tube face was occupied by a prism (P) at 50 cm. that served to align the image of the moth next to that of the tube face. Since both images were at the same distance from the camera, the centimeter scale on the tube face (Fig. 2 *et seq.*) serves both as a time base for the echo trace and a size scale for the image of the moth.

Grouped as closely as possible around the prism were the sound source (S)—an ultrasonic transducer of the capacitative type with a membrane of 0.5 mil metallized Mylar, a Granath microphone (M) operating on the same principle, and the flash unit of a Grass PS1 Photo Stimulator (F). All three units were aimed as precisely as possible at a point to be occupied by the moth 50 cm. distant and at right angles to the camera-oscilloscope axis. The apparatus was aimed acoustically as well as visually by placing a 1-cm. sphere at this point and maximizing the echo picked up by the microphone. An attempt was made to place the axes of the microphone and transducer in relation to the optical axis so that the optical profile of the moth would correspond as closely as possible to that presented to the sound pulse.

In most of the experiments the ultrasonic pulses were between 70 and 90 kcps, 0.7 millisecond in duration, and with about 0.2 millisecond rise and fall time. Frequency modulation, of the sort encountered in the pulses of vespertilionid bats, was not employed. The ultrasonic pulses were formed by clipping the output of an oscillator (OSC.) by means of an electronic switch (General Radio). The "on" (A) and "off" (B) commands to the switch were the synchronizing and stimulus pulses from a Grass S4 stimulator. Thus, the ultrasonic pulse duration was controlled by the stimulus delay circuit of the stimulator. The flash contact in the camera triggered the stimulator each time a frame was exposed. The ultrasonic pulses thus formed passed through an attenuator and amplifier to the transmitter. In some of the experiments the signal leaving the attenuator was monitored on the lower beam (Y 2) of the oscilloscope. The sweep of the latter was triggered by the A pulse from the stimulator. A sweep speed of 1.0 millisecond/mm. was used throughout.

The A pulse also triggered the electronic flash after passing through a delay circuit. The delay was needed to insure that the image of the moth was photographed at the instant the sound pulse reached it. The picture thus reveals the moth's attitude in flight at the moment the sound pulse was reflected from its wings and body. Since the moth was approximately 50 cm. distant from the sound source the flash was delayed by 1.6 milliseconds. The duration of the flash was approximately 10 microseconds.

The microphone used to detect the echo was connected through its amplifier and a band-pass filter (to eliminate extraneous noise) to the upper beam (Y 1) of the oscilloscope.

Moths of various species were captured at light. They were mounted by cementing the mesonotum with Tackywax to an insect pin. The pin was attached to a thin vertical support of bamboo. Pin and support alone gave a negligible echo. No other object stood for a radius of several feet behind the moth, but little trouble was experienced with extraneous echoes, owing to the brevity of the pulses and the high sweep speed. The click of the camera shutter produced some acoustic interference, but this arrived later than the echo and could be disregarded.

Most moths flew spontaneously, and often for considerable periods, as soon as a paper wedge in contact with the tarsi was removed. The procedure was to take a sequence of frames at random as the moth continued to fly. Sixty to 70 frames covered most of the wing positions for a given angle of presentation. Each frame

was exposed for 0.01 second. The opening of the camera shutter via the cable release triggered the onset of the ultrasonic pulse, the sweep, and, after an appropriate delay, the flash. The lower trace in each frame displays the shape of the signal and the upper trace displays its echo as detected by the microphone.

Some direct interaction took place between transmitter and microphone. This occurred because a fairly intense pulse was needed in order to get an adequate echo from the moth, and because it was necessary to place transmitter and microphone as close as possible above and below the prism so as to minimize the disparity between the optical and acoustic reflections. The signal caused by this interaction appears as the first pulse on the upper trace of each recording, and serves as another control of the outgoing signal. During a given experiment it remained constant. The second signal on the upper trace, occurring about 2.5 milliseconds after the direct pulse, is the echo returned by the moth while it was in the attitude shown by the accompanying flash picture.

The still camera was replaced in later experiments by a 16-mm. motion picture camera equipped with a telephoto lens. The rotating shutter was equipped with a wiping contact that closed momentarily during the exposure of each frame. This triggered the stimulator, sound pulse, and flash as before. The camera (Ensign) was a spring-driven model, about 35 years old, in which the film speed was found to vary with the amount of pressure applied to the release button. This defect made it possible to obtain satisfactory stroboscopic pictures. With the moth in flight the camera speed was gradually increased until the number of frames per second approached the wingbeat frequency (commonly between 15 and 35 per second) of the moth. This was determined by watching the image of the moth revealed by the flashes of the strobe light. The large number of frames made available by the motion picture was of great value in the analysis.

In view of what has been said (Roeder, 1962) about the behavior of moths in the presence of ultrasound it may seem paradoxical that the moths continued to fly while being bombarded by high-intensity ultrasonic pulses. Indeed, at the beginning of a run they frequently ceased flying as soon as the sound sequence began. Some specimens were discarded as being too refractory or erratic. However, continued exposure to sound appeared to adapt the neural mechanism responsible for evasive behavior, and in most cases the moths flew steadily after a few false starts. It is fairly certain that many of the recorded wing attitudes included abrupt changes in angle of attack and amplitude associated in free moths with erratic flight. These and similar departures from "normal" flight movements are also to be expected from the restrained condition of the subjects. This problem of studying natural wing movements in insects restrained for observation has long plagued students of insect aerodynamics.

Echoes were recorded from the following species: *Sunira bicolorago* Gn., *Amphipyra pyramidoides* Gn., *Agrotis ypsilon* Rott., *Enargia decolor* Wlk., *Ennomos magnarius* Gn., *Amathes c-nigrum* L., *Graptolitha unimoda* Lintner, and *Orthosia hibisci* Gn.

## RESULTS

Figure 2 shows certain attitudes and their corresponding echoes when the axis of a flying moth is approximately at right angles to the sound path. At this



angle the largest echo is produced when the wings are near the top of the stroke (A). The smallest echo is produced during the latter part of the downstroke (C), while echoes of intermediate size occur at the beginning of the downstroke (B) and near its end (D). The maximum echo produced near the top of the wing stroke is dependent upon a critical wing angle. This caused it frequently to be missed when single frames were taken. The stroboscopic motion picture method not only made a much greater number of single frames available, but it was also possible by manipulating the camera speed to hold a particular wing attitude for a number of consecutive frames. Figure 3A illustrates the contrast in magnitude

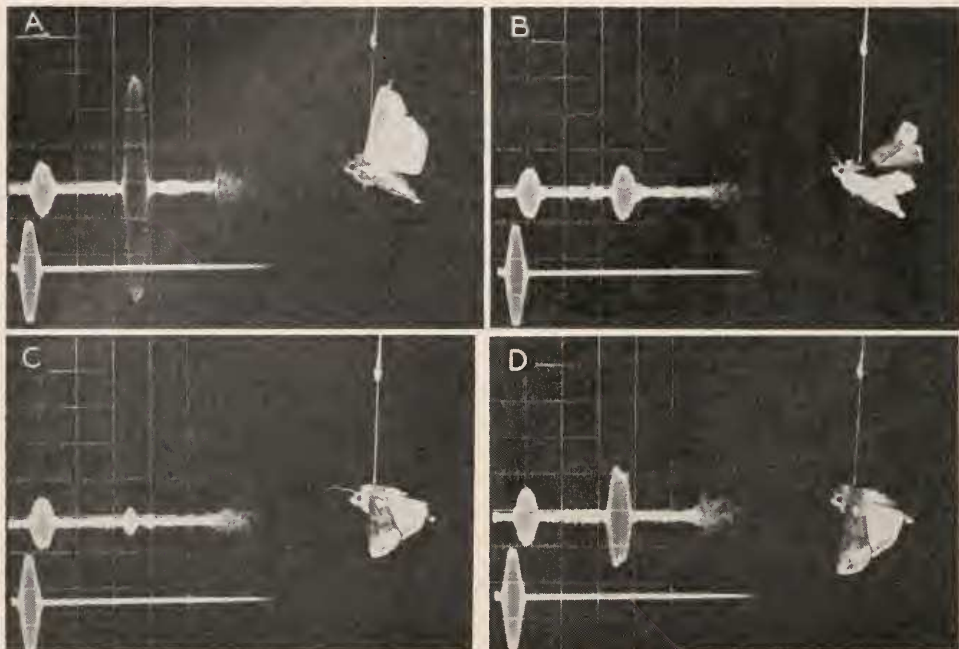


FIGURE 2. Echo and attitude of *Agrotis ypsilon* in fixed flight on bearing about  $90^\circ$  to sound path. Ultrasonic pulse 78 kcps, 0.7 msec. in duration. Grid on oscillogram equals 1.0 msec. on trace, 1.0 cm. on photograph. A, top of wing stroke; B, first half of downstroke; C, last half of downstroke; D, bottom of stroke. See text for other details.

between minimum and maximum echoes produced during the last half of the upstroke. In this series also the maximum echo appears to be produced when the surface presented by the wings is about  $90^\circ$  to the sound path. An attempt to hold the optically determined attitude of the moth constant at this point by adjusting the camera speed produced a series of attitudes that show little optical difference, although the size of the echo fluctuates widely (Fig. 3B).

From this it can be concluded that the body of the moth plays a negligible part in causing an echo, most of the acoustic reflection coming from the surface of the wings presented at  $90^\circ$  to the sound path. This effect may at times be further accentuated by the slightly curved surface assumed by the wings at the beginning of the downstroke. This maximum echo must occur either once or

twice in rapid succession near the top of the stroke, depending upon the amplitude of the stroke and upon the precise angle of the moth relative to the sound path.

Recordings made with the axis of the potential flight path at other angles to the sound path showed similar fluctuations of echo with wingbeat, but the size of the maximum echo never reached that recorded when the axis of the

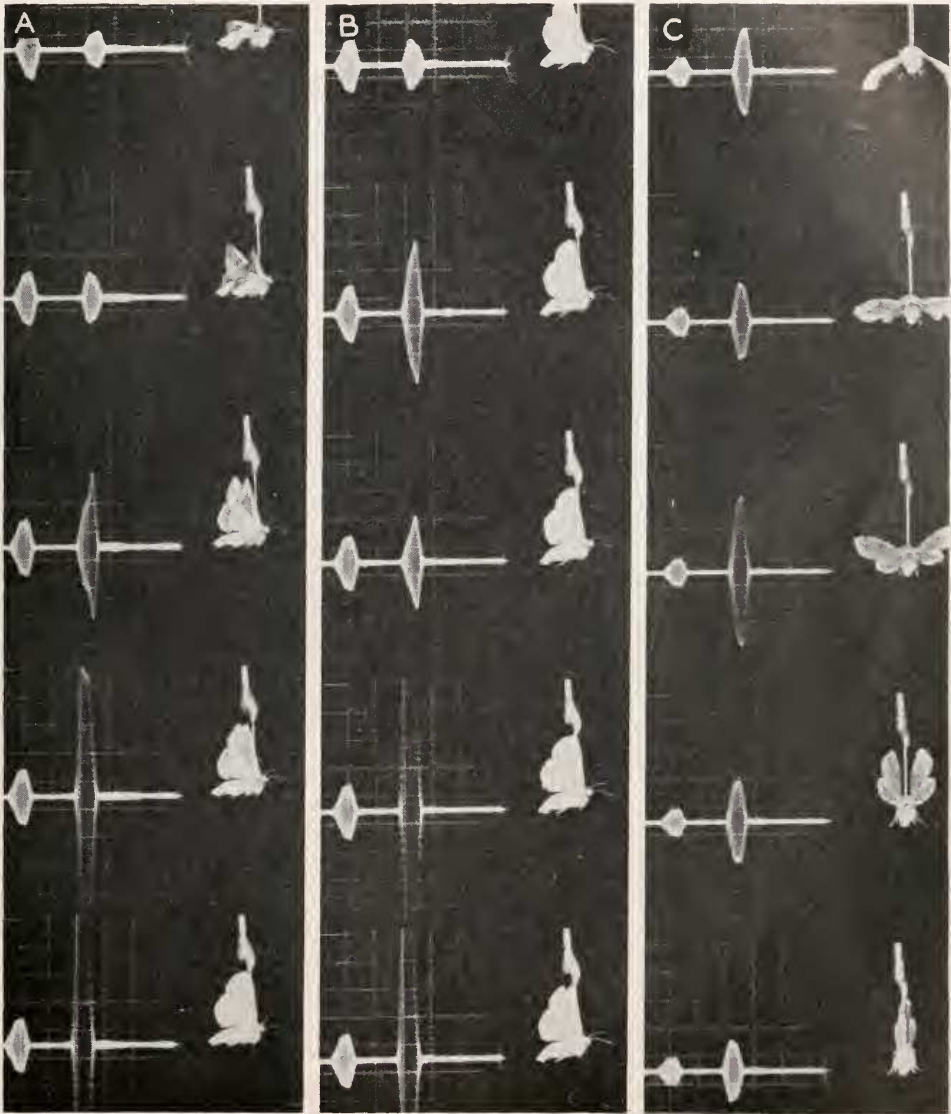


FIGURE 3. Consecutive frames from motion picture of echo and attitude of flying *Orthosia hibisci*. Ultrasonic pulse 85 kcps, 0.7 msec. in duration. Grid equals 1.0 msec. on oscillogram, 1.0 cm. on photograph. A, the second half of the upstroke. B, image held nearly stationary in stroboscopic sequence. C, path of moth directly away from sound source, wings in phases of upstroke.

moth was approximately  $90^\circ$  to the sound path. Samples of echoes from other angles are shown in Figure 3C, where the moth is headed directly away from the sound source, and in Figure 4, where the course is about  $135^\circ$ .

In the present experiments the moth was always mounted as if it were in level flight at the same altitude as the optical and acoustic system. Since the surface of the wings appears to be the main source of echoes, it is apparent from the photographs, particularly those of Figure 4, that maximal echoes would be

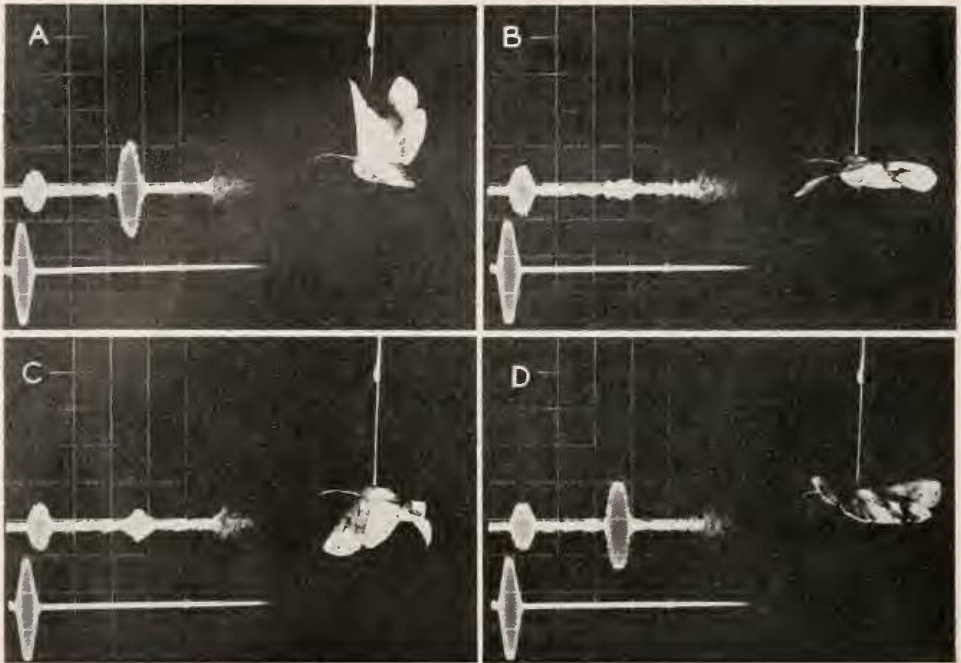


FIGURE 4. Echo and attitude of *Agrotis ypsilon* on course about  $135^\circ$  away from sound source. Other details as in Figure 2. A, early in downstroke. B, mid downstroke. C, early in upstroke. D, mid upstroke.

returned from other wing positions and flight angles if the transmitter and microphone were aimed at the moth at various angles from above or below the plane of flight. These were not investigated.

During a given run the peak echoes usually went off the oscilloscope screen (Fig. 3B) while minimum echoes sometimes disappeared in the noise level of the recording system. This made it difficult to estimate with any accuracy the intensity difference between maximum and minimum echo. In many cases it was certainly greater than 20 to 30 decibels.

Distortions of the echo were also common. The echo shown in Figure 5A has essentially the same form as the outgoing pulse. The asymmetric peak in B was probably due to movement of the wings towards the attitude producing a maximum echo during the interval of time (0.7 millisecond) that the pulse impinged upon them. The sharp peak shown in C indicates that the attitude

producing a maximal echo was reached only briefly near the midpoint of the pulse. The double peaks shown in D and E may have been due to the opposite effect, the wings passing through an attitude of minimum echo during the pulse. Another possible explanation of the double peaks shown in D and E is suggested by the attitudes of the wings shown in the photographs. Echoes may have been produced separately by the near and far pair of wings. A difference in the length of the sound path from one of the two reflecting surfaces to the source by 0.5 or 1.5 wave-lengths might be expected to produce partial or complete interference and extinction of the echo. For an 82 kcps pulse of 4 mm. wave-length, such interference would occur when the wings were 1.0 or 3.0 mm. apart. This cannot be measured from the photographs, but the dimensions of the moth make it entirely possible.

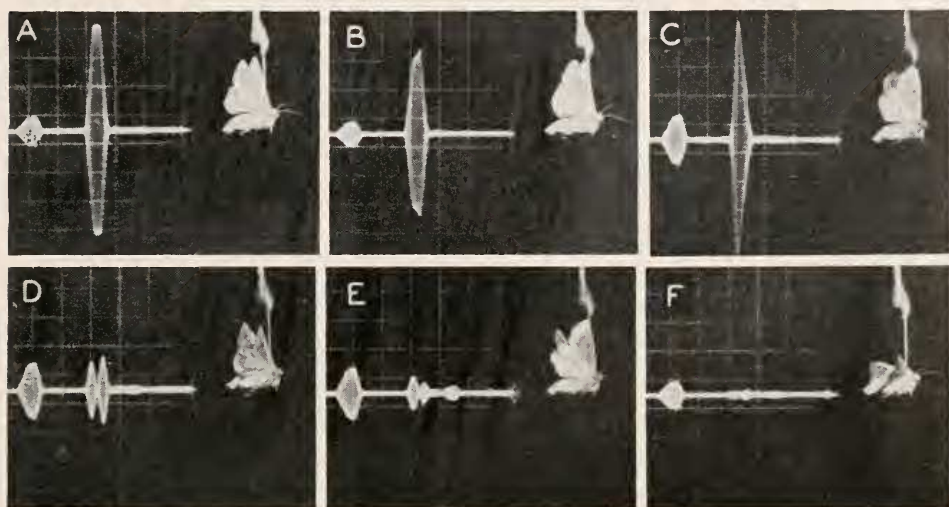


FIGURE 5. Distortions in the echo returned by *Orthosia hibisci*. Other details as in Figure 3. A, echo showing minimal distortion. B, distortion due to movement of wings to point of greater reflectance during impact of pulse. C, sharp peak caused by wings moving through position of maximum reflectance during pulse. D and E, double echoes; see text. F, abnormally small echo.

A similar explanation may account for cases where the minimum echo is below the noise level or possibly absent (Fig. 5F). Occasionally, as in D and E, a small pulse appears somewhat more than a millisecond later than the main echo. The origin of this is unknown.

Some speculation has centered on the functional significance of the scales that typically cover the wings and body of Lepidoptera. The setae covering the thorax may be extremely dense and filiform, forming a deep "fur" in many noctuids, such as *Leucania pseudargyria*. In other species, particularly in certain arctiids, this coat of scales may be very thin or almost absent, yet moths of both families and with all degrees of thoracic vestiture have well-developed tympanic organs (Haskell and Belton, 1956; Roeder and Treat, 1957) and are presumably subject to attack by bats.



A few measurements were made of the effect of this covering of scales on the echoic qualities of the subjects of the present study. Amputated wings were statically mounted so as to produce a maximum echo. They were then denuded of scales with an artist's paintbrush and the echo re-measured. Similar treatment was given to wingless bodies. Removal of the scales increased the echo by 1 or 2 decibels. Since this is an insignificant figure compared with that produced by changes in wing angles during normal flight, it was concluded that the scales play an unimportant role in reducing the echoic qualities of moths.

#### DISCUSSION

From one point of view it might seem that these results demonstrate merely what could have been predicted from an elementary knowledge of the laws of wave motion. There is some comfort in this to the biologist accustomed to the unexpected in living things. The size of the echo from the wings in the attitude normal to the sound path compared with that produced by the body and the wings in other attitudes shows that the acoustic profile of a flying moth goes through much greater extremes than does its optical profile. Assuming that a bat were equipped only with a crude sonar system of the sort used in these experiments, the most definitive information that it would receive would be that its prey was flapping its wings. An optical comparison is suggested by the scintillations produced by suspended microscopic crystals, such as mica. However, in the biological situation occupied by the hypothetical bat and a flying moth, the scintillations would occur at regular intervals determined by the wingbeat frequency of the insect, and they would be maximal only when their source was travelling on certain bearings relative to the flight path of the bat.

It is certain that this postulated situation is a gross over-simplification, particularly with respect to the acoustic capabilities of the bat. Nevertheless, it does suggest some points that may have relevance in connection with the behavior of flying moths when exposed in the field to a sudden train of ultrasonic pulses (Roeder, 1962). When close to the ultrasonic source or when exposed to pulses of high intensity many moths react by changing from a relatively straight flight path to a variety of turns, spirals, and dives. Others close their wings and fall passively to the ground. The experiments reported here suggest that cessation of flight movements and closure of the wings must eliminate the major source of echoes, as well as the echo fluctuation characteristic of flight, thereby providing the insect with some measure of acoustic concealment as it falls to the ground.

In the same paper it was reported that moths flying at greater distances from the sound source and exposed to lower intensities frequently turned from their flight path and flew directly away from the sound source. This maneuver has the obvious advantage to the moth in putting distance between it and its potential predator, but the echo experiments suggest that it may have additional survival value. Moths flying at roughly the same altitude as an approaching bat are most likely to present an optimum target for echoes if they cross the flight path of the bat at about  $90^\circ$  (see Fig. 3). The first clue available to a bat approaching at maximum range must be a very brief echo of its cry occurring once or twice for each wingbeat of the target. Since at least some noctuid moths are certainly

capable of detecting the echolocating cries of a bat at a considerably greater range than a bat can detect their echoes (Roeder and Treat, 1961), it must be of some advantage to the moth to assume a less echo-producing flight path, *e.g.*, parallel to or directly away from that of the bat, as soon as the latter has been detected.

The situation is much more difficult to assess from the viewpoint of the bat, for its frequency-modulated cry is more complex than the pulses used in these experiments and little is known about its capabilities of acoustic discrimination. Relatively long pulses, such as the cruising pulses emitted by *Myotis lucifugus* (Griffin, 1958), might increase the bat's chances of picking up a brief maximal echo from a flying moth. For instance, a cry 15 milliseconds in duration would last throughout one half of the wingbeat, *i.e.*, for the whole upstroke or downstroke, of a moth flapping its wings 30 times a second. The echo returning to the bat would be amplitude-modulated with a sharp peak at one point. At extreme range the brief peak would be the only part of the echo detected by the bat.

Detection of an echo causes most bats to increase the repetition rate of their cries to as much as 150 per second. At the same time there is a decrease in the duration (to 1.0 millisecond or less) and in the frequency (to about 25 kcps) of each pulse of sound. Most noctuid moths have wingbeat frequencies of between 10 and 40 per second. Therefore, when reception of an echo causes the bat to increase its pulse repetition rate a point must be reached where there is phasic interaction between pulse frequency and echo frequency determined by the moth's wingbeat. At some frequencies the phasing of pulse and echo source would produce a maximal echo every time, while at others the echo would be missed entirely. The signal significance of this effect, as well as the role played by frequency modulation in the bat's cry, cannot be estimated at present.

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Some of the equipment was loaned by Professor Donald R. Griffin of Harvard University. The moths used were identified by Dr. Asher E. Treat of the City College of New York.

#### SUMMARY

1. Moths of several species were mounted in stationary flight and the echoes of ultrasonic pulses were recorded simultaneously with flash photographs of the attitude assumed by the wings at the instant the pulse reached the insect.

2. The largest echo was produced by moths flying at the same altitude as the sound source when the potential course was roughly at right angles to the sound path and the wings were near to the top of the stroke. The difference between this maximum echo and that produced by the body and wings at other attitudes of the wing stroke was 30 decibels or more.

3. Moths flying at the same altitude as the sound source but on other courses produced echoes that fluctuated with wing position. However, the maximum was never as great as that registered on the 90° course.

4. Distortions in the shape of the echo are described and their causes are discussed. Scales on the wings or body of the moth do not appear to play an important anechoic role.

5. It is concluded that the plane surface of the wings returns the major portion of the echo. The significance of this is discussed in relation to the problems of detection and evasion encountered under natural conditions by bats and flying moths.

#### LITERATURE CITED

- GRIFFIN, DONALD R., 1958. Listening in the Dark. Yale University Press, New Haven, Conn.
- GRIFFIN, DONALD R., FREDERIC A. WEBSTER AND CHARLES R. MICHEL, 1960. The echolocation of flying insects by bats. *Animal Behaviour*, **8**: 141-154.
- HASKELL, P. T., AND P. BELTON, 1956. Electrical responses in certain lepidopterous tympanic organs. *Nature*, **177**: 139-140.
- KOLB, A., 1958. Über die Nahrungsaufnahme einheimischer Fledermäuse vom Boden. *Verh. Deutsch. Zool. Gesellsch. in Frankfurt a.M.*, 162-168.
- MÖHRES, F. P., 1950. Aus dem Leben unserer Fledermäuse. *Kosmos*, **46**: 291-295.
- ROEDER, KENNETH D., 1962. The behaviour of free flying moths in the presence of artificial ultrasonic pulses. *Animal Behaviour*, **10**: 300-304.
- ROEDER, KENNETH D., AND ASHER E. TREAT, 1957. Ultrasonic reception by the tympanic organ of noctuid moths. *J. Exp. Zool.*, **134**: 127-158.
- ROEDER, KENNETH D., AND ASHER E. TREAT, 1961. The detection and evasion of bats by moths. *Amer. Sci.*, **49**: 135-148. (Reprinted in 1961 Annual Report of Smithsonian Institution.)
- TREAT, ASHER E., 1955. The response to sound in certain Lepidoptera. *Ann. Ent. Soc. Amer.*, **48**: 272-284.
- WEBSTER, FREDERIC A., 1963. Bat-type signals and some implications. Human Factors in Technology (eds., E. Bennett, J. Degan, and J. Spiegel). McGraw-Hill Book Co., Inc., New York, N. Y.
- WEBSTER, FREDERIC A., AND DONALD R. GRIFFIN, 1962. The role of the flight membranes in the capture of insects by bats. *Animal Behaviour*, **10**: 332-340.